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Research paper

The palaeoecological value of *Diporotheca rhizophila* ascospores (Diporothecaceae, Ascomycota) found in Holocene sediments from Lake Nussbaumersee, Switzerland

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ABSTRACT

Lake Nussbaumersee, a medium-sized lake SW of Lake Constance (Switzerland) and well known for its Neolithic and Bronze Age pile-dwelling settlements, provides invaluable insights into the possible interpretation of *Diporotheca rhizophila* ascospores (Diporothecaceae, Ascomycota) in palaeoecological studies. Calcareous gyttja sediments from a 7500 yrs old stratigraphy were analysed palynologically, resulting in statistical correlations of *Diporotheca* spores with pollen and non-pollen palynomorphs (NPPs). Positive correlation existed with arboreal taxa such as *Corylus avellana* and *Acer*, herb taxa such as *Allium*, and aquatic taxa such as *Anabaena* (Cyanobacteria) and *Filinia* eggs (Rotifera). Negative statistical correlation was shown between *Diporotheca* and the arboreal taxa *Quercus* and *Betula*, Poaceae and Cyperaceae, and the fern *Pteridium aquilinum*. These results suggest that ecological indicator values for the root parasite *D. rhizophila* may not only be closely related to the autecology of its common host *Solanum*, but that *D. rhizophila* may generally be an indicator of major soil disturbance and extensive soil erosion due to the impact of agricultural activities by prehistorical people, as well as due to livestock trampling of wetlands and lake shore ecosystems.

1. Introduction

Lake Nussbaumersee, situated in the region southwest of Lake Constance (Switzerland; Fig. 1), is well known for its Neolithic and Bronze Age pile dwellings (Hasenfratz and Schnyder, 1998). Lake sediments therefore allow palynological and palaeoecological research on how prehistorical societies and their livestock influenced their environment. During the last 25 years three lakeside settlements in and around Lake Nussbaumersee were excavated and dendrochronologically dated to the Neolithic and to the Bronze Age (Fig. 1). The Neolithic settlement "Inseli" from the Pfyner Culture is one of the longest lasting pile-dwelling settlements all over Central Europe for this time period and existed from 3840 BC to at least 3700 BC (Hasenfratz and Schnyder, 1998). Vegetation-historical aspects since the Late Glacial and the influence of prehistorical pile-dwelling societies on the surrounding flora and vegetation of Lake Nussbaumersee were the subject of the first palynological studies focussing on pollen, cryptogam spores and some selected non-pollen palynomorphs (Rösch, 1985; Haas and Hadorn, 1998). Given the significant alterations on the upland flora during the Neolithic shown in the study by Haas and Hadorn (1998), major follow-up research was recently initiated on the prehistoric human impact on past littoral wetland and lake ecosystems of Lake Nussbaumersee using detailed analysis of locally produced non-pollen palynomorphs from the same sediment samples. Indeed, research on non-pollen palynomorphs (NPPs) has received increasing attention as they have proven to be highly useful in palaeoecological reconstructions (van Geel, 2003; Haas, 2010). However, NPP-analysis is still not a standard method in palaeoecological research, due to the dearth of identification keys, identification problems and often poorly known environmental indicator values. In addition, many of these microfossils are significantly smaller than most pollen and therefore more difficult to detect.

Ascospores of the fungus *Diporotheca rhizophila* (Diporothecaceae, cf. Lumbsch and Huhndorf, 2007 and Index Fungorum Partnership, 2012) are about the size of medium-sized pollen grains (47–52 × 17–25 µm; van Geel et al., 2003) and can therefore easily be counted during standard palynological analyses. These spores (often also named as NPP type HdV-143 in the palynological literature; Fig. 2) are very distinctive by their surface with dark brown anastomosing ribs and their two large pores and tapering ends, but they may have different shapes as mature and immature spores can be released from one perithecium (Gordon and Shaw, 1960). Such ascospores were first described from Holocene sediments by van der Wiel (1982) who placed them under the

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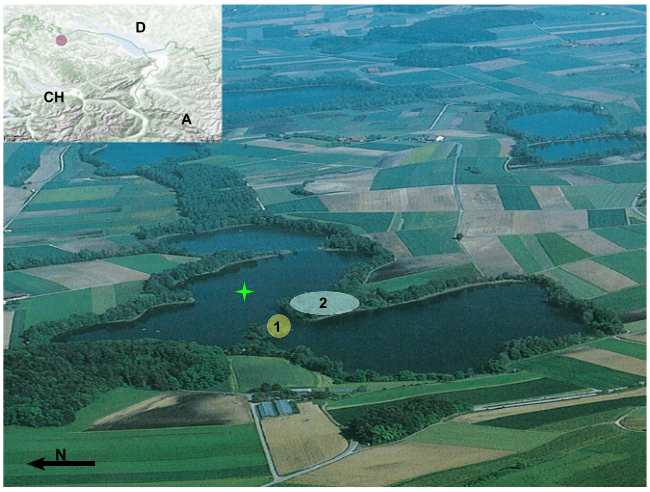

Fig. 1. The research area of Lake Nussbaumersee in NE Switzerland (inset map, upper left). The Neolithic pile dwelling settlement "Inseli" is shown with a yellow circle (1), the location of the Late Bronze Age settlement "Ürschhausen-Horn" is shown in blue (2). The coring point is indicated by a green star. (Abbreviations: CH: Switzerland, A: Austria, D: Germany.) Photo by P. Nagy, Winterthur.

unidentified fungal spore type 143. Then, van Geel et al. (1986) identified the type as *Diporotheca* sp. and van Geel and Aptroot (2006) recently recognised it as *D. rhizophila* C.C. Gordon and C.G. Shaw.

Diporotheca is widespread all over the world, as spores were not only found in palaeoecological studies of Eemian and Holocene sediments in Europe, but have also been described from lake sediments on the American and African continents (van Geel et al., 1986, 2011; Almeida-Lenero et al., 2005; Gelorini et al., 2011). The genus currently includes two species (*Diporotheca litseae* M.S. Patil and *Diporotheca rhizophila* C.C. Gordon and C.G. Shaw), whereby only *D. rhizophila* is known to occur on plants native to Europe.

Diporotheca rhizophila is known to be a parasite on the roots of *Solanum* species (nightshade family; Gordon and Shaw, 1960). In Europe this fungus grows especially on roots of *Solanum nigrum* which mainly grows under wet meso- and eutrophic conditions in disturbed environments such as forest openings, alder carrs, reed belts, and as ruderals or on agricultural fields (Ellenberg and Leuschner, 2010). For this reason, findings of spores of *D. rhizophila* have often been seen as indicative for past and extant nutrient rich, eutrophic wetland conditions (e.g. Ramezani et al., 2008; Montoya et al., 2010; Wheeler et al., 2010), which were often interpreted to be the result of human influence. Although other host–parasite relationships are up to now not known for *D. rhizophila* from the mycological literature, some palynological studies argued for other possible hosts, such as the wetland fern *Thelypteris palustris* because of analogies in the past frequency of occurrences (van Geel et al., 1986; van Geel and Aptroot, 2006).

In this paper we present correlations between Holocene *Diporotheca* ascospores and pollen and other non-pollen palynomorphs in order to get a better understanding of their value as palaeoenvironmental indicators for Quaternary palynological studies.

2. Materials and methods

2.1. Study site

The valley of Seebachtal is located to the southwest of Lake Constance in the Swiss Canton of Thurgovia (Thurgau) and was formed during the Last Glacial period (Würm). Nowadays, the Seebachtal valley contains three lakes of which Lake Nussbaumersee is the westernmost (Fig. 1). Its lake level is at about 434 m a.s.l., and the lake surface area is approximately 27 ha, with a maximum water depth of about 8 m. Lake Nussbaumersee is divided into three separate basins currently connected with each other, but which were separated during the Early Holocene due to isostatic rebound and climatic change (Hasenfratz and Schnyder, 1998). Today, remnants of a Magnocaricion (dominated by *Carex elata*) and of an Alno-Ulmion alder carr forest with *Alnus glutinosa* (alder), several *Salix* (willow) species and *Frangula alnus* (alder buckthorn) characterise the vegetation zones along the shores of the lake. The upland vegetation is dominated – apart from large agricultural fields – by *Fagus*

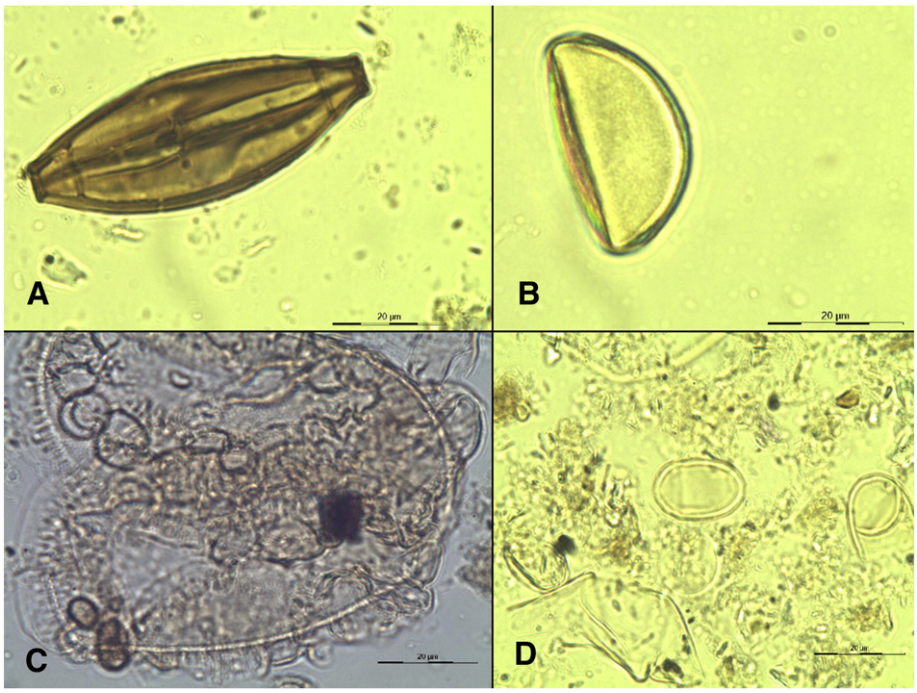

Fig. 2. Selected NPPs and pollen from the Holocene sediments of Lake Nussbaumersee (Switzerland). A: *Diporotheca rhizophila*, B: *Allium* sp., C: *Filinia* sp., D: *Anabaena* sp. (length of bar: 20 µm).

sylvatica (beech) forests (Fig. 1), which exist on stony–clayey soils since beech immigration about 7000 years ago (Haas and Hadorn, 1998).

2.2. Archaeological settings

Thanks to intensive studies by archaeologists and palaeoecologists, the prehistory of the area of Lake Nussbaumersee is quite well known (Haas and Hadorn, 1998; Hasenfratz and Schnyder, 1998). Three main lakeside settlements (Fig. 1) below and just above today's water level were excavated and dendrochronologically dated to the Neolithic Period (3840 to at least 3700 BC; Pfyner Culture), the Late Early Bronze Age (1580–1538 BC) and to the Late Bronze Age (ca. 850–800 BC). The Neolithic pile-dwelling village (Nussbaumersee-"Inseli") was formerly lying on a land bridge between the north-western and south-eastern lake shores, and was inhabited for at least 140 years. In spite of the medium size of the village (with approximately 30 houses) a major forest opening was recognised by palynological means, while the much bigger Late Bronze Age lakeside village "Ürschhausen-Horn" (with more than 100 buildings) showed comparably little impact on the surrounding vegetation (Haas and Hadorn, 1998).

2.3. Palynological settings

A calcareous gyttja sediment core (NBS-1993; with a total length of 950 cm) was taken in 1993 from the deepest point of Lake Nussbaumersee using a Livingstone type corer (Fig. 1; geographical coordinates: 47° 36′ 52″ N/8° 49′ 20″ E). Thereafter sediment sub-samples of 1 cm^3 each were taken at four centimetre steps for palaeoecological analyses, whereby the uppermost 230 cm (representing the Medieval Period and the Modern Times) was not analysed. All sediment samples were prepared for palynological study following standard procedures (Moore et al., 1991), including sediment sieving through a 200 μm mesh sieve (to separate microfossils from macrofossils) and by applying a 1-minute acetolysis, but no hydrofluoric acid (HF) treatment. *Lycopodium* spores were added to determine the concentration of microfossils (Stockmarr, 1971). Apart from pollen and cryptogam spores studied earlier (Haas and Hadorn, 1998), all non-pollen palynomorphs (NPPs) were counted from the same sample residues. Detailed NPP analysis was generally done at 8 cm steps, with exception of the Neolithic settlement phase, where samples were analysed at 4 cm intervals. NPPs were identified and counted using a light microscope (at a magnification of 600×). All NPP types were determined using mycological and palynological literature (Lundqvist, 1972; van Geel, 1972; Pals et al., 1980; van Geel et al., 1981, 1989, 1996, 2003; Barthelmes et al., 2006; van Geel and Aptroot, 2006), as well as the reference collection of the Hugo de Vries Laboratory (HdV, University of Amsterdam, The Netherlands).

Haas and Hadorn (1998) counted a minimum of 500 pollen grains per sample and calculated the percentage of each taxon in comparison to the defined 100%-pollen sum (= total of arboreal and non-arboreal pollen, excluding pollen from aquatics, as well as fern and moss spores). For the quantification of NPPs presented in this study between 15 and 85 *Lycopodium* spores were counted depending on palynological concentrations, resulting in 140 to more than 1500 non-pollen palynomorphs per sample (average 576). In samples with very high numbers of certain types (i.e. *Anabaena* and *Aphanizomenon*) these types were only counted to a lower number of *Lycopodium* spores and then extrapolated. Using the *Lycopodium* counts in each sample and the defined pollen sum by Haas and Hadorn (1998), the NPP influx values and percentages in relation to the defined 100% pollen sum were calculated. The percentage values of selected taxa are presented using Tilia version 1.7.16 software (Grimm, 2011).

2.4. Statistical analysis

To test the correlation between *Diporotheca* spores and all pollen and other non-pollen palynomorphs taxa, a bivariate correlation test was performed on percentage values using SPSS 18 software (IBM, New York, NY, USA) calculating the Pearson coefficient in a two-sided correlation. Since the samples in the stratigraphy are not independent of each other, partial correlations controlling for several abundant variables (total tree pollen, diatoms, microscopic charcoal, total fungal spores) and showing no correlation with *Diporotheca*, were also calculated.

2.5. Radiocarbon dates

A first series of 12 AMS-radiocarbon dates was performed on terrestrial macrofossils in 1994–1997 at the ETH Zürich, Switzerland (Table 1; see also Haas and Hadorn, 1998) and recently, four additional

Table 1
List of ^{14}C-dates performed on terrestrial plant macrofossils from the calcareous gyttja sediment core of Lake Nussbaumersee (Switzerland). Dates in italics were not used for the chronological interpolation (see Fig. 3). Calibration of radiocarbon dates was done using IntCal09 and OxCal v4.1.7 (Reimer et al., 2009; Bronk Ramsey, 2010). Most probable ages are given according to the Clam-model run on original ^{14}C-dates (Blaauw, 2010). (Abbreviations: BS = bud scales, C = catkin parts, L = leaf parts indet, S = seeds, SL = substantia lignosa indet.)

Depth (cm)	Sample no.	^{14}C date	Delta ^{13}C	Age calibrated (mean ± 2σ)	Most probable age (Clam model)	Material dated
88–90	ETH-41472 (UZ-5920)	75 ± 40 BP	−61.1 ± 1.1	**AD 1809 ± 127**	**AD 1821**	SL
246–248	ETH-17753	1455 ± 60 BP	−24.6 ± 1.2	**AD 550 ± 120**	**AD 585**	*Fagus sylvatica* BS
253.5–262.5	*ETH-14265*	*2500 ± 95 BP*	*−2.7 ± 1.2*	*605 ± 205 BC*		*Alnus glutinosa* S, SL
316.5–325.5	*ETH-11845*	*2905 ± 55 BP*	*−28.7 ± 1.1*	*1095 ± 175 BC*		*Alnus glutinosa* S, *Betula* sect. *alba* S, *Betula pendula* S, *Fagus sylvatica* BS
374–376	ETH-41473 (UZ-5921)	2600 ± 70 BP	−73.7 ± 1.1	**714 ± 201 BC**	**720 BC**	*Alnus* sp. C, BS indet.
424.5–430.5	*ETH-14266*	*3385 ± 75 BP*	*−22.7 ± 1.3*	*1700 ± 190 BC*		*Alnus glutinosa* S, *Betula pubescens* S, SL
446–448	ETH-41474 (UZ-5922)	3115 ± 55 BP	−78.6 ± 1.1	**1362 ± 140 BC**	**1379 BC**	*Fagus sylvatica* BS
472.5–475.5	*ETH-14267*	*3900 ± 80 BP*	*−19.8 ± 1.2*	*2355 ± 225 BC*		*Alnus glutinosa* S, L
476–478	ETH-41475 (UZ-5923)	3360 ± 55 BP	−74.1 ± 1.1	**1684 ± 178 BC**	**1651 BC**	*Alnus* sp. C, L
559.5–562.5	ETH-11846	3970 ± 50 BP	−29.7 ± 1.1	**2455 ± 165 BC**	**2482 BC**	*Alnus* sp. C
610.5–613.5	ETH-11847	4405 ± 60 BP	−30.6 ± 1.2	**3120 ± 220 BC**	**3081 BC**	*Alnus* sp. C
631.5–640.5	*ETH-11848*	*4785 ± 90 BP*	*−19.9 ± 1.2*	*3540 ± 180 BC*		*Alnus* sp. C, *Alnus glutinosa* S, *Tilia* sp. BS, bark remains
692.5–704.5	ETH-11849	4830 ± 65 BP	−20.8 ± 0.9	**3570 ± 200 BC**	**3604 BC**	*Alnus* sp. C, *Alnus glutinosa* S, *Betula pubescens* S, *Betula* sect. *alba* S
775.5–784.5	ETH-11850	5460 ± 60 BP	−27.7 ± 1.1	**4265 ± 195 BC**	**4304 BC**	*Alnus glutinosa* S, *Alnus* sp. C, *Tilia* sp. BS
878.5–881.5	ETH-11851	6045 ± 60 BP	−32.4 ± 1.2	**4995 ± 215 BC**	**4955 BC**	SL
943.5–949.5	ETH-11852	6665 ± 65 BP	−29.7 ± 1.1	**5595 ± 115 BC**	**5586 BC**	*Alnus* sp. C, *Alnus glutinosa* S, *Tilia* sp. BS

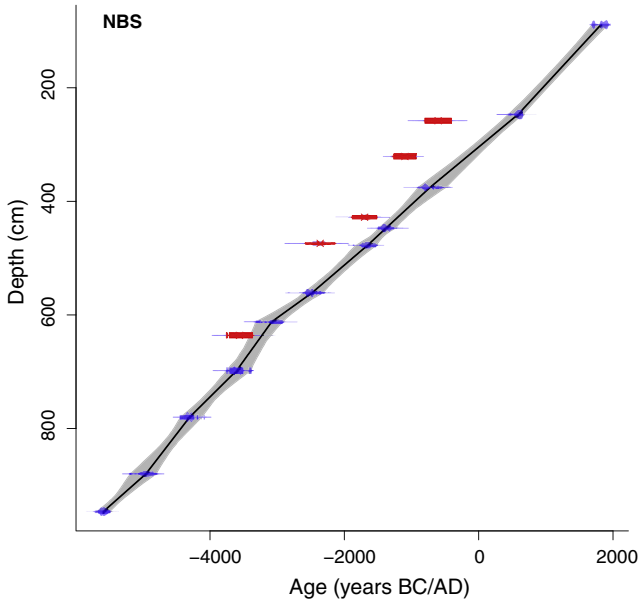

Fig. 3. Age–depth model for the sediments of Lake Nussbaumersee (Switzerland) using the Clam model (Blaauw, 2010). Radiocarbon dates not used for the chronological interpolation are crossed out.

AMS-radiocarbon dates were obtained from the same Institute after pre-treatment at the Geographical Institute of the University of Zürich (UZ; Table 1). Five ^{14}C-dates were excluded for the linear chronological age interpolation as they were viewed as less reliable compared to the obtained relative ages of corresponding pollen data. The final age–depth model (Fig. 3) was created using Clam software (Blaauw, 2010). This age–depth model shows a near linear relation between age and depth in the part of the sediment core used for NPP analyses and was subsequently used for the interpretation of the palynological results using Tilia software (Grimm, 2011; Fig. 4). Given the age–depth model we therefore assume an almost unvarying sedimentation rate in the deepest, central part of the lake from ca. 5500 BC to AD 1800 (corresponding to 948–88 cm sediment depth; Fig. 3).

3. Results

3.1. Palynology

A diagram of selected pollen and NPP types from the Lake Nussbaumersee stratigraphy (NBS) is shown in Fig. 4. Pollen data showed a significant increase of non-arboreal (herb) pollen percentages between ca. 3900–3600 BC (740–700 cm depth) which must be attributed to Neolithic agricultural activities, especially in connection with the pile-dwellers from 3840 to 3700 BC (Haas and Hadorn, 1998; Hasenfratz and Schnyder, 1998). With the newly obtained NPP results, several lake water eutrophication phases can be detected. These are (inter alia) represented by peaks of Cyanobacteria (especially *Aphanizomenon* and *Anabaena*; Fig. 2), which are very probably a result of high nutrient input by the lakeside people (van Geel et al., 1994). *Diporotheca rhizophila* thereby peaked from about 3790 to 3560 BC (720–692 cm sediment depth) which corresponds well with the Neolithic pile-dwelling phase (Nussbaumersee-"Inseli"). Both after and before this period, *Diporotheca* is present in most samples in very low percentages, except for the lowermost parts of the sediment core, where percentages were higher.

3.2. Statistical analysis

Correlation tests (Table 2) resulted in significant positive correlations of percentages of *Diporotheca* spores with several pollen and non-pollen palynomorphs: Highly significant correlations were found with *Anabaena* (Cyanobacteria), which also shows a peak in the Neolithic Period as well as *Filinia* eggs (Rotifera). Highly significant correlations exist also with tree pollen of *Corylus avellana* (hazel) and the herbal taxon *Allium*. Significant positive correlations of *Diporotheca* is shown with *Acer* pollen (maple) and the hitherto unknown NPP type cf. HdV-182. On the other hand, *Diporotheca rhizophila* presence is negatively correlated with the arboreal taxa *Quercus* (oak) and *Betula* (birch), as well as with Poaceae, Cyperaceae, and *Pteridium aquilinum* (bracken). None of the other 260 pollen and NPP taxa from this study showed any significant correlation with *Diporotheca*. Partial correlations controlling for several variables (total tree pollen, diatoms, microscopic charcoal, total fungal spores) were calculated since samples in the stratigraphy are not independent of each other. The results differed very slightly from the correlations originally calculated, so only a selection is shown in Table 2.

4. Discussion

Diporotheca rhizophila is known as a mildly pathogenic fungus, parasitical on the surface of roots of several *Solanum* species (Mibey and Hawksworth, 1995). Our results leave room for two different interpretations, which may both be valid to a varying degree in different geographical and climatic settings.

4.1. Host species

The ascospore finds from the sediments of Lake Nussbaumersee showed no correlation with *Solanum* pollen, which is probably due to the fact that wild, insect pollinated *Solanum* species produce a relatively small amount of pollen which is weakly dispersed. This is a common feature, as several palaeoecological studies with *Diporotheca rhizophila* spores in their palynological preparations did not find any (or very few) pollen of *Solanum* species (e.g. van Geel et al., 2003). The plant macrofossil analysis of the Lake Nussbaumersee sediment core did not provide any evidence of *Solanum* seeds or leaves either (Hillbrand, data not shown). However, the palaeoethnobotanical study of the cultural layers from the Neolithic pile-dwelling settlement Nussbaumersee-"Inseli" (3840–3700 BC) revealed that these layers contained several seeds of *Solanum dulcamara* and *Solanum nigrum* (Hillbrand, unpublished data), which confirms the growth of *Solanum* species in the vicinities of Lake Nussbaumersee. So, we assume that the peak in *Diporotheca* may be related to the regular presence of Solanaceae on agricultural fields, forest clearings or reed belts during the Neolithic. The positive correlation of *D. rhizophila* spores with *Allium* pollen might point to the near-lake presence of a fen wood or of beech (*Fagus sylvatica*) forests, both the typical ecosystems where e.g. *Allium ursinum* must have been dominant during Neolithic times, as also known from other prehistorical settings in Switzerland (Hadorn, 1994; Haas and Hadorn, 1998). This would also be the habitat where *S. dulcamara* occurs (Ellenberg and Leuschner, 2010) which would favour the growth of *Diporotheca*. This could explain why several palynological studies show a visible relation between *Alnus* or *Salix* and *Diporotheca* (e.g. Bos et al., 2005; Gelorini et al., 2006; Menozzi et al., 2010; Deforce, 2011). Prager et al. (2006) studied modern non-pollen palynomorphs from three different alder carrs and found that *D. rhizophila* lies inside a group of NPPs representative of wet conditions with mosses. So, an alder carr may have been present around Lake Nussbaumersee during periods of wet climate before and after the Neolithic settlement period as indicated by high values of *Alnus* (Fig. 4). In this context, and although there is no correlation between *Alnus* pollen and *Diporotheca* spores in the sediment core from Lake Nussbaumersee, the results of the plant macrofossil analysis from the same core showed a significant correlation between *D. rhizophila* spores and *Alnus* macrofossils (seeds and catkin-scales > 250 µm; see Fig. 4).

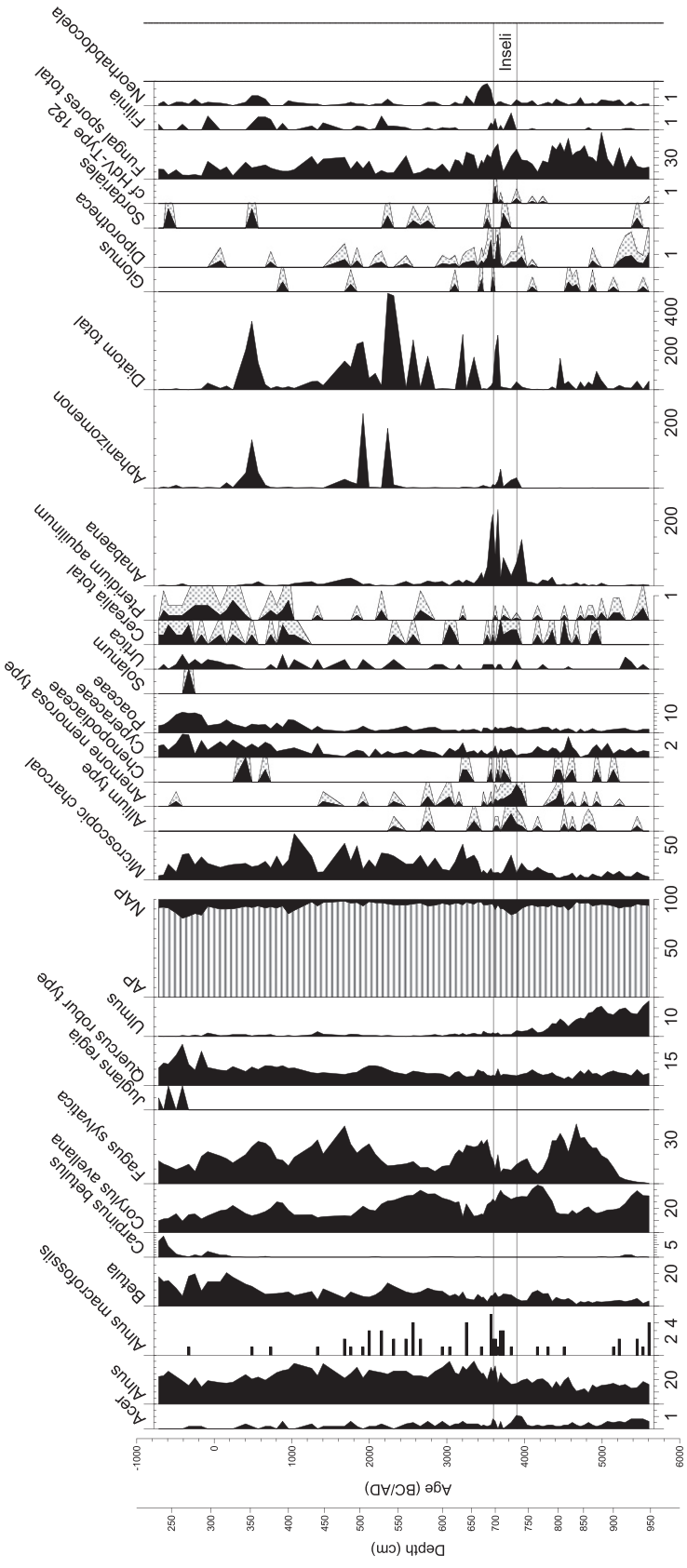

Fig. 4. Palynological percentage diagram (selected pollen and NPP taxa) obtained on the calcareous gyttja stratigraphy of Lake Nussbaumersee (Switzerland). *Alnus* macrofossils (>250 μm) are shown in absolute numbers. The lines indicate the approximate chronological position of the dendrochronologically dated Neolithic pile-dwelling settlement of Lake Nussbaumersee-"Inseli". Exaggeration percentage curve (3×) is shown in white for selected taxa. Where no labels are shown on the x-axis, the tic marc represents 0.5%. (Abbreviations: AP = arboreal pollen, NAP = non-arboreal pollen.)

Table 2
Statistical correlations (Pearson coefficient) between *Diporotheca rhizophila* ascospore finds and selected pollen and non-pollen palynomorphs taxa (percentages) and partial correlations corrected for indicated factors from the Holocene sediments of Lake Nussbaumersee (Switzerland).

Taxon	Significance	Correlation coefficient	Partial correlation (significance) corrected for:		
			Diatoms	Charcoal	Fungal spores indet
Positive bivariate correlation					
Anabaena	0.000**	0.669	0.667 (0.000)	0.669 (0.000)	0.670 (0.000)
Corylus	0.009**	0.263	0.259 (0.010)	0.264 (0.009)	0.269 (0.008)
Allium	0.006**	0.274	0.280 (0.005)	0.273 (0.007)	0.274 (0.007)
Filinia	0.010**	0.260	0.260 (0.010)	0.267 (0.008)	0.265 (0.009)
cf Type 182	0.015*	0.246	0.247 (0.015)	0.245 (0.016)	0.247 (0.015)
Acer	0.047*	0.201	0.200 (0.049)	0.201 (0.049)	0.200 (0.049)
Negative bivariate correlation					
Betula	0.029*	−0.221	−0.217 (0.032)	−0.220 (0.030)	−0.240 (0.018)
Quercus	0.030*	−0.219	−0.225 (0.027)	−0.218 (0.032)	−0.229 (0.024)
Pteridium	0.032*	−0.217	−0.229 (0.024)	−0.218 (0.032)	−0.216 (0.034)
Cyperaceae	0.038*	−0.210	−0.214 (0.035)	−0.209 (0.040)	−0.210 (0.039)
Poaceae	0.044*	−0.204	−0.218 (0.032)	−0.215 (0.034)	−0.206 (0.043)

N = 98.
** Highly significant (<0.01).
* Significant (<0.05).

On the other hand, in a study of modern NPPs performed in the Pyrenees Mountains (Cugny, 2011), *Diporotheca rhizophila* spores were found in moss samples from small, grazed wetlands, while they were absent in the mosses taken from adjacent terrestrial ecosystems (beech forests, clearings, heathland, grasslands). The only two sites where *Solanum* species were present in the local vegetation of this study were terrestrial sites where no *D. rhizophila* ascospores were found. Therefore we support the hypothesis proposed by van Geel et al. (1986) and van Geel and Aptroot (2006) that other host plants may exist for *D. rhizophila*, such as the wetland fern *Thelypteris palustris*. *Thelypteris palustris* also grows mainly in alder carr and similar habitats which leads us to suggest that even if *Solanum* is not found in pollen studies, the presence of *Diporotheca* is likely to indicate the existence of habitats where *Solanum* species and – as our results and comparisons with other studies indicate – mainly *Solanum dulcamara* grow (i.e. wet and nutrient rich conditions).

4.2. Erosion

The growth of *Diporotheca* on roots in the soil means that *Diporotheca* spores are probably mainly dispersed by soil erosion. In the Pyrenees *Diporotheca rhizophila* spores were most abundant in a wet zone highly trampled by livestock (Cugny, 2011). This suggests that soil disturbance, and subsequent extensive soil erosion might be decisive for the presence of *D. rhizophila* ascospores in wetland soils, and subsequently also in palynological samples from lake sediments. Taking these considerations into account, the high input of *Diporotheca* spores in Lake Nussbaumersee was probably due to the increased soil erosion and agricultural run-off, resulting in the highly significant positive correlation of *Diporotheca* with *Anabaena* and *Filinia* due to related rising lake water nutrient levels (eutrophication). This hypothesis is supported by the findings of *Glomus* which show no statistical correlation with *Diporotheca* but usually occur together with *Diporotheca* spores (Fig. 4). In addition, soil disturbance is indicated by the highly significant correlation between *Diporotheca* ascospores and pollen from shrubs and trees such as *Corylus avellana* and *Acer*, quickly and intensively growing within disturbed forest ecosystems and on abandoned agricultural fields. The negative statistical correlation of *D. rhizophila* with grasses (Cyperaceae and Poaceae), trees (*Quercus* and *Betula*) and ferns (*Pteridium aquilinum*) probably indicates that closed forests have prevented the erosion of soil in periods with low human impact and, subsequently, the spreading of ascospores of *D. rhizophila* towards the lake. This may therefore have led to an under-representation of *Diporotheca* in the palynolo-gical data set during times of low anthropogenic pressure.

In summary, high values of *Diporotheca rhizophila* ascospores may indicate (1) distinctive, local prehistorical soil disturbance and extensive erosive input of soil matter towards Lake Nussbaumersee and (2) the existence of wet and eutrophic habitats where hosts of *Diporotheca* grow. So, spores of this fungal genus may generally be a valuable disturbance indicator for prehistorical human and livestock activities in the wetlands and forests adjacent to lakes, as well as for disturbances and erosion processes within semi-opened landscapes (agricultural field systems) favouring the dispersal of spores of *Diporotheca*. On the other hand our study – once again – was not able to show any significant correlations between *Solanum* species and *Diporotheca*, which leads us to support the theory that the fungus may have other possible hosts (van Geel et al., 1986). These hosts, however, would probably have a similar autecology as *Solanum* species, but remain to be detected by future mycological research. Nevertheless, ascospores of *D. rhizophila* should be seen as an indicator for meso- to eutrophic and often wet habitats, combined with major soil disturbance and extensive erosion processes, which in turn may help to enlighten the structure and composition of prehistorical landscape features and past environments.

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